

GENETIC AND MORPHOLOGICAL RELATIONSHIPS OF THE TEXAS ENDEMIC *RUELLIA DRUMMONDIANA* (ACANTHACEAE)

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The genus *Ruellia* is represented by approximately 20 species in the United States that may be conveniently placed into 3 sections following the classification offered by Lindau (1895): sect. *Dipteracanthus*, represented by *R. caroliniensis* (J. F. Gmel.) Steud., and *R. humilis* Nutt. of southeastern and midwestern distribution respectively, characterized by axillary, nearly sessile flowers with straight corolla tubes; sect. *Eruellia*, represented by *R. occidentalis* (A. Gray) Tharp and Barkley of wide distribution in Texas, with flowers in terminal racemes, and corolla tubes slightly bent; and sect. *Physiruellia*, represented by *R. malacosperma* Greenm. and *R. brittoniana* Leonard, both taxa introduced and naturalized from Central America and West Indies, with large flowers on long, axillary peduncles. *Dipteracanthi* and *Eruelliae* produce fruits with mostly 6-10 seeds per capsule; *Physiruelliae* produce longer capsules with 16-20 seeds.

One of the taxonomically most perplexing species among *Dipteracanthi* is *R. drummondiana* (Nees) Gray (Fig. 1). The plant was first described by Nees as *Dipteracanthus drummondianus* based on a specimen collected by Drummond in Texas "between Brazosia and San Felipe" (DeCandolle, 1847). Nees said that in certain characters the species resembled the widespread Midwestern species *R. strepens* L., differing chiefly in having linear sepals and in being uniformly pubescent. It can be added that *R. drummondiana* differs from all other U. S. species in normally having only 2-4 seeds per fruit, rather than 6-20 of other taxa. In this respect the species resembles *Dyschoriste* and, except for the absence of characteristic anther appendages, it might be confused with species of this genus. Gray (1878) transferred *D. drummondianus* Nees to *Ruellia* but made no comment regarding any apparent morphological relationships for the plant, nor do Tharp and Barkley (1949) suggest affinities within the genus. In addition to morphological distinctiveness, *R. drummondiana* is endemic to east-central Texas where it is partially sympatric with *R. caroliniensis*, *R. humilis*, *R. strepens* and *R. occidentalis*.

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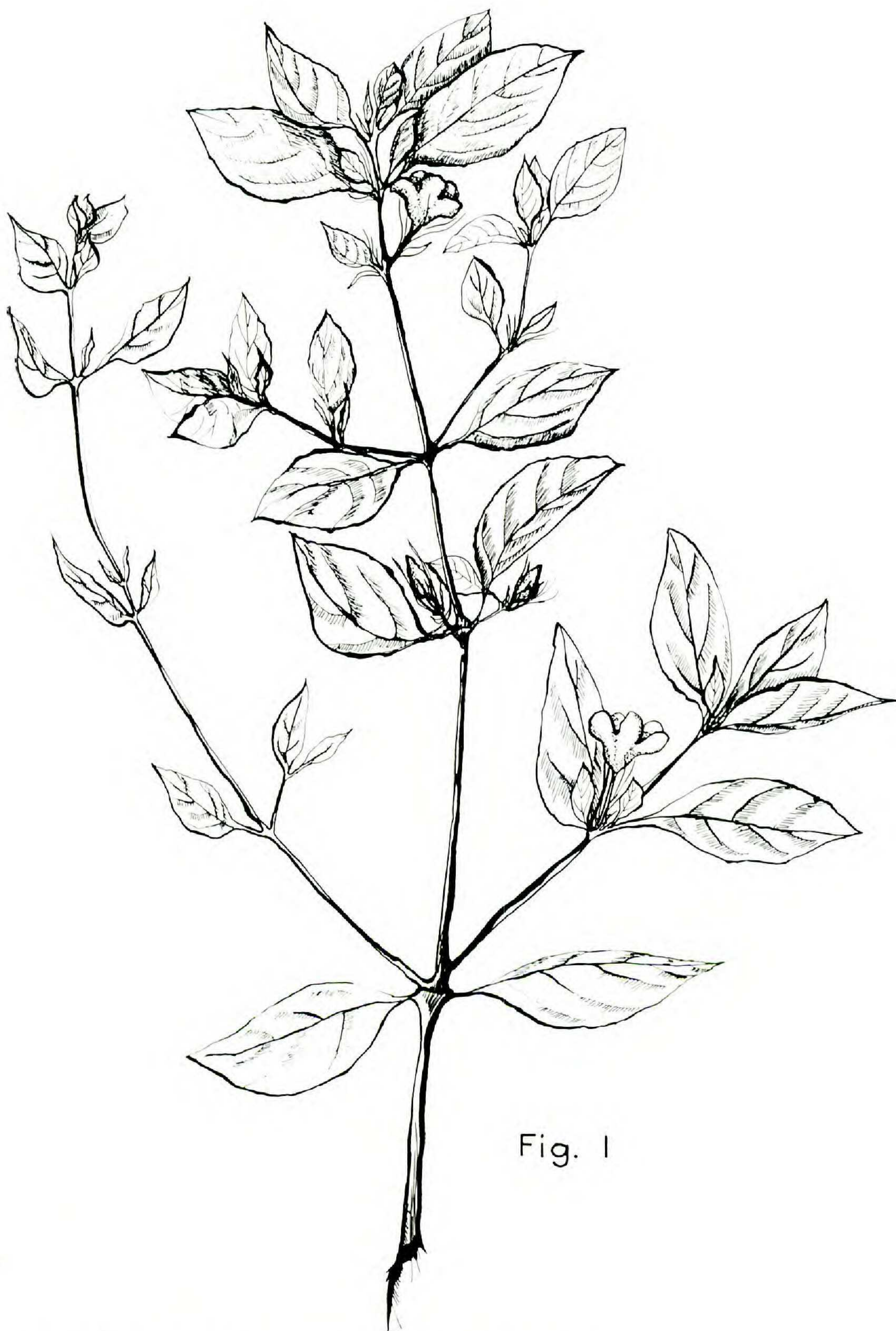


Fig. 1

Fig. 1. *Ruellia drummondiana*, approx. $\times \frac{1}{2}$.

MORPHOLOGICAL COMPARISONS.—The following paragraphs will summarize the nature of various structures in *R. drummondiana* with observations and comments on similarities and differences with other U.S. species.

The plants grow erect from a fibrous, wiry root-system composed of laterals that tend to grow from a single crown at the base of the stem. Roots may be fleshy and slightly thickened near the stem base. These characters are found throughout U.S. *Dipteracanthi*. Stems are herbaceous, green or dark-green, ridged, and canescent-pubescent, usually simple but with branching arising near the base if optimum growth conditions are present. Leaves are opposite, generally decussate, broadly ovate-truncate but with the blade partially decurrent on a definite petiole. Blades are dark-green and softly canescent especially along the veins. *Ruellia drummondiana* resembles *R. strepens* more closely than any other species in general leaf morphology.

Flowers are produced singly in upper leaf axils, subsessile or on short peduncles, they are large and conspicuous with slight bilateral symmetry because the lower corolla lobe forms a lower "lip", and the upper 4 extend radially outwards. *Ruellia drummondiana* generally resembles *R. pedunculata* Torr. of the Ozark plateau and certain populations of *R. humilis* in corolla shape. Another useful character of the corolla is the pigment pattern: heavier streaks of dark-brown color are found on the lip with lighter radial streaks extending between the lobes in *R. drummondiana* resulting in an asymmetric pigment pattern. This character is also found in *R. humilis* and *R. pedunculata*, but a symmetric pattern with 5 even radial streaks extending into the lobes is found in *R. caroliniensis*.

The sepals are linear-subulate, usually about 1-2 mm. wide at the base. The morphology clearly places *R. drummondiana* with *R. humilis*, *R. caroliniensis* and all other U.S. *Dipteracanthi* excepting *R. strepens* which has broad, foliaceous sepals 4-5 mm. wide. A very useful character in classifying *Ruelliae* that apparently has been overlooked is the position of the stamens and relative length of filaments. In *R. drummondiana* the didymous stamens are clustered together below the upper corolla lobe, and each pair has one filament longer than the other. These characters are found in *R. humilis*, and also in other taxa such as *R. occidentalis* and *R. malacosperma*, but not in *R. caroliniensis* where stamens are not clustered but are alternate with corolla lobes and filaments are approximately of equal length.

Another very useful character is the morphology of the stigma: *R. drummondiana* essentially has 1 stigma branch, again resembling *R. humilis*, *R. occidentalis*, *R. malacosperma*, *R. pedunculata* and *R. strepens* as well, but differing from *R. caroliniensis* which has two equal stigma branches. Artificial hybrids between species with 1 and with 2

stigma branches produce $1\frac{1}{2}$ stigma branches. Obviously natural hybrids could be detected by examination of stigma morphology. Capsules of *R. drummondiana* contain 2-4 seeds but frequently there are no fertile seeds owing to seed-abortion and insect depredation. Total reproductive capacity of plants appears to be very low, judging from behavior of plants grown in garden cultures.

BREEDING SYSTEM.—*Ruellia drummondiana* resembles all U.S. species in being completely self-compatible but nevertheless producing large, conspicuous, colored flowers that are visited by bees, moths, and butterflies. Long styles are exerted and the stamens inclosed well within the throat of the corolla in an arrangement obviously adapted to cross-pollination. In addition to the chasmogamic forms, very small, tubular, greenish-white cleistogamous flowers are produced either before, during, or after chasmogamic flowering. It is now known that cyclic cleistogamy occurs in all U.S. species (Long and Uttal, 1962; Long, unpubl.). Both kinds of flowers may form fruit in *R. drummondiana*, and judging from observations made in the greenhouse and garden neither appears to be a more effective seed-producer than the other. This is in sharp contrast with *R. strepens* which is strongly cleistogamic, having a short, ineffective chasmogamic phase followed by a prolonged, seed-prolific cleistogamic phase. Greenhouse cultures of *R. strepens* were strictly cleistogamic making it impractical to test compatibility with plants of *R. drummondiana*. In *R. caroliniensis*, *R. succulenta* Small, *R. heteromorpha* Fernald and other southeastern species-populations, chasmogamic flowering is prolonged, cleistogamy occurring later and of shorter duration; both flower-forms appear to be equally seed-prolific although local ecological factors strongly influence conditions of flowering. The method of seed dispersal is by sudden opening of matured capsules resulting in the propulsion of seeds for short distances. In general *R. drummondiana* appears to fall between the types of effective breeding systems of *R. strepens* and of *R. caroliniensis*. The preponderance of seeds produced are formed by cleistogamic flowers, a fact that is evident when one examines local populations. The conditions that determine the type of breeding system are probably ecological in nature. From the standpoint of reproductive biology the plant should be classified as a facultative cleistogamic species (Uphof, 1938) or, perhaps more accurately, a facultative inbreeder (Fryxell, 1961). Cleistogamic or chasmogamic flowering occurs in response to moisture or nutritional stress similar to that reported for *Bromus* (Harlan, 1945) and for *Stipa* (Brown, 1952). Lack of effectiveness of chasmogamy, the relatively small number of seeds per fruit, frequent capsule abortion, relatively slow seed germination and consequent difficulty in becoming established may account in part for the restricted range for the species.

ARTIFICIAL HYBRIDIZATIONS.—During the past three years an

extensive artificial hybridization program has been carried out in *Ruellia* in order to obtain information regarding genetic relationships of the species, and to get some estimate of the possible role of natural hybridization in generating variation within and between species by comparing artificial hybrids with population samples. A further aim of these investigations was to determine chromosomal homologies of species but this has been only partially successful owing to the small size of chromosomes and difficulty in obtaining and staining appropriate meiotic figures. A summary of the results of these hybridization experiments and cytological observations together with sources of materials and techniques of hybridizing and growing hybrid *Ruellias* has been presented elsewhere (Long. 1966).

Table 1 lists interspecific artificial hybridizations that involve *R. drummondiana* as one of the parental species. Fertile, vigorous hybrids were produced with *R. caroliniensis*, *R. humilis*, *R. heteromorpha*, and *R. succulenta*. Intermediate morphological characters were noted especially in stem vestiture, leaf size and pubescence, petiole length, corolla size and symmetry, and stigma morphology. Character dominance apparently occurs in such features as corolla pigment markings and stamen position. Table 2 presents a detailed comparison of the morphological characters of *R. caroliniensis* × *R. drummondiana*, and *R. humilis* × *R. drummondiana* hybrids and the parental species. In these hybrids character intermediacy can be noted in general habit, leaf size,

parental species	no. pollinations	no. plump capsules	no. seeds produced	% seed germination	no. F1 produced	% non- stainable pollen range
<u>R. drummondiana</u> X						
<u>R. caroliniensis</u>	6	1	6	66	4	10-24
<u>R. drummondiana</u>	7	6	20	91	18	19-52
<u>R. heteromorpha</u>	5	5	21	71	15	5-16
<u>R. humilis</u>	3	2	8	88	7	15-21
<u>R. malacosperma</u>	9	0	--	--	--	--
<u>R. occidentalis</u>	3	3	16	56	7	no pollen
<u>R. pinetorum</u>	2	1	0	--	--	--
<u>R. succulenta</u>	5	2	20	30	6	17-35

Table 1. Artificial hybridization experiments involving *Ruellia drummondiana*. (Measurements for both tables made from greenhouse-grown plants; voucher specimens deposited in the U.S.F. Herbarium.)

petiole length, sepal length, corolla length and symmetry, and stigma morphology.

Sterile, weak F_1 hybrids were formed by the intersectional cross *R. drummondiana* \times *R. occidentalis*. These plants have persisted in greenhouse culture for 2 years but have never produced flowers. No hybrids were formed in crosses with the southeastern coastal plain endemic *R. pinetorum* Fernald or with *R. malacosperma*.

DISCUSSION.—A biosystematic classification of U.S. species of sect. *Dipteracanthus*, i.e., one based on crossability, hybrid sterility, and ecological adaptation as well as morphological comparisons, results in the grouping of taxa into at least 4 polytypic ecospecies: (1) *R. caroliniensis*, and closely related southern Florida endemics *R. succulenta* and *R. heteromorpha*; (2) *R. humilis*; (3) *R. strepens*, and the related Appalachian endemic *R. purshiana* (Uttal, 1965); and, (4) *R. pedunculata* and the related coastal plain endemic *R. pinetorum* (Long, 1966). Additional ecospecies may be recognized as work progresses, but these 4 constitute the most important sources of variation. The results of hybridization experiments lead me to conclude that *R. drummondiana* is related genetically to both *R. caroliniensis* and *R. humilis* ecospecies. Fertile, vigorous F_1 hybrids are produced when these plants are crossed with *R. drummondiana*. Garden-grown hybrids of *R. humilis* \times *R. drummondiana* are unusually vigorous and they spread aggressively; hybrids of *R. caroliniensis* \times *R. drummondiana* are somewhat less vigorous, and 2 did not survive into the second year. Preliminary examination of meiotic configurations during microsporogenesis indicates chromosome pairing is normal in artificial hybrids, with only an occasional chain of four chromosomes. We may conclude, therefore, that the chromosomes are closely homologous.

The morphological evidence leads me to believe that *R. drummondiana* is more closely related to *R. humilis* than to *R. caroliniensis* or *R. strepens*. Pubescence patterns, corolla symmetry and pigmentation, stamen size and position, and stigma morphology are closely similar for both species. Thus, *R. drummondiana* appears to be morphologically a well-marked element of the *R. humilis* ecospecies, but one also having close genetic relationships with *R. caroliniensis* that suggest affinities for both ecospecies.

Before concluding this report it may be useful to consider the problem of endemism in *Ruellia* with special reference here to *R. drummondiana*. Fryxell (1962) has defined an endemic as one with a relatively restricted range which may be (1) a young, expanding species; (2) an evolving but not expanding species ("stationary endemic"); (3) a contracting relict

Table 2. Morphological comparisons of parental species and their artificial hybrids in *Ruellia*.

character	<u>caroliniensis</u>	<u>drummondiana</u> X <u>caroliniensis</u>	<u>drummondiana</u>	<u>drummondiana</u> X <u>humilis</u>	<u>humilis</u>
culture no.	(60-35)	(63-107w X 60-35)	(63-107w)	(63-107w X 64-329)	(64-329)
stem:					
general habit	erect, few laterals	erect, branching from base	erect, branching from base	decumbent, spreading	decumbent
maximum height	41.5 cm.	20.0 cm.	23.0 cm.	14.1 cm.	28.5 cm.
vestiture	glabrous	glabrous	hirsute	hirsute	hirsute
leaf:					
maximum length	4.7	4.8	8.5	4.5	6.2
maximum width	1.8	2.6	5.0	2.4	2.5
leaf index	0.45	0.54	0.59	0.53	0.40
vestiture	puberulent on veins	generally strigose	canescent	canescent	hirsute on veins
petiole length	0.7	0.8	1.0	0.3	0.0
flower:					
maximum sepal length	1.4	2.0	2.9	2.0	2.0
sepal vestiture	few short hairs	ciliate	canescent	carely ciliate	ciliate
maximum corolla length	4.7	3.8	4.0	3.5	2.8
corolla symmetry	radial	nearly radial	bilateral	nearly bilateral	nearly radial
corolla pigment markings	radial	stronger on lowest lobe	stronger on lowest lobe	stronger on lowest lobe	stronger on lowest lobe
stamen position	alt. with lobes	paired convergent below upper lobes	convergent below upper lobes	convergent below upper lobes	convergent below upper lobes ₁
stigma branches	two equal	1 short, 1 long	1	1	

species. Stebbins (1942) has suggested that lack of variability was one characteristic of endemic species. The morphological uniformity of *R. drummondiana* populations may be accounted for on the assumption of predominant autogamy, although outbreeding may occur, and the apparent genetic homogeneity of the species is a reflection of effective breeding system rather than a character of the species because it is endemic. Stebbins' genetic explanation of the basis of endemism cannot account for restricted distributions of certain other species of *Ruellia*, as *R. succulenta* and *R. heteromorpha*, where local populations may be morphologically uniform or highly variable, apparently depending on predominant breeding system, availability of new habitats, and proximity of related populations that may result in introgression (Long, 1964). The lack of variability in *R. drummondiana* and certain other *Ruellia* endemics cannot be based on genetic incapacity that results in lack of variability, but rather is dependent on the ecological factors that affect breeding systems. Morphological uniformity does not appear to be a causative factor of endemism in *Ruellia* (cf. James, 1961).

Any discussion of endemism should include not only the genetic approach to factors affecting population structure, but also the historical factor relating to geological events and past distributions. *Ruellia* is largely a tropical and subtropical group of plants that probably belonged to the Neotropical-tertiary flora that ranged northward into southern United States from the Antilles, Central America, and Mexico. In eastern United States most of the warm temperate and subtropical species had been eliminated by Miocene times, and the retreat of this flora left numerous relict species with Neotropical affinities (Chaney, 1947). The center of variation of North America Dipteracanthi is in Southeastern U.S.; this suggests that they may have entered Texas from the north rather than from Mexico. The present distribution of *R. drummondiana* is near the Balcones Fault on the Edwards Plateau, a position that places it on the southern periphery of the range for *R. humilis*.

Natural populations of *R. drummondiana* observed thus far have all been relatively small in number, usually composed of approximately 20-30 individuals and all morphologically very similar except for minor differences probably caused by ecological factors. An examination of the collections in the University of Texas Herbarium showed that the plant may be found in roadside areas, near footpaths, in dry stream beds and in similar disturbed areas where selection pressure is at a minimum. The total evidence leads to the conclusion that *R. drummondiana* is a "stationary endemic", or more likely, a "relict species" that was once part of a much larger and more varied population system that is now also represented by numerous races of *R. humilis*. Endemism in U.S. species of *Ruellia* also includes examples of "young, expanding" endem-

ics as *R. heteromorpha* and *R. succulenta*, as well as stationary or relict endemics as *R. drummondiana*, and perhaps others such as *R. purshiana* and *R. pinetorum*.

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